HYRACODONS FROM THE BIG BADLANDS OF SOUTH DAKOTA.

Investigation aided by a grant from the Marsh Fund of the National Academy of Sciences.

By WILLIAM J. SINCLAIR.

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Introduction.

Studies in progress at Princeton on the *Mesohippus bairdii-Oreodon culbertsoni* zone of the White River Oligocene, typically developed in the Big Badlands of South Dakota, have made necessary an examination of specific characters in the genus *Hyracodon,* considered as an index fossil, and also a review, in this connection, of a recent paper on the subject by Mr. Troxell.[1]

The Four Specific Types.

Four distinct types can easily be recognized as follows:

A. With the end of the protoloph curving round the end of the metaloph in p^4 and completely fusing therewith in worn teeth, isolating a central depression. Inner wall of tooth not deeply grooved. Anterior cross-crest in p^1 present, but may be small and little more prominent than the cingulum. Fig. 1.

B. With the transverse valley of p^4 blocked by a spur from the protoloph which abuts against the anterior wall of the metaloph. The latter cross-crest is longer than the former in unworn teeth, but tends to shorten up as the tooth wears. Inner wall of tooth deeply indented; p^1 with anterior cross-crest present or absent. Fig. 2, *A–C.*

C. Transverse valley of p^4 wide open; p^1 with anterior cross-crest small or absent. Fig. 3, *A, B.*

D. Transverse valley of both p^4 and p^3 wide open. Anterior cross-crest in p^1 of variable size. Figs. 4, 5.

[1] "New Species of Hyracodon," *American Journal of Science,* II., July, 1921, pp. 34–40.

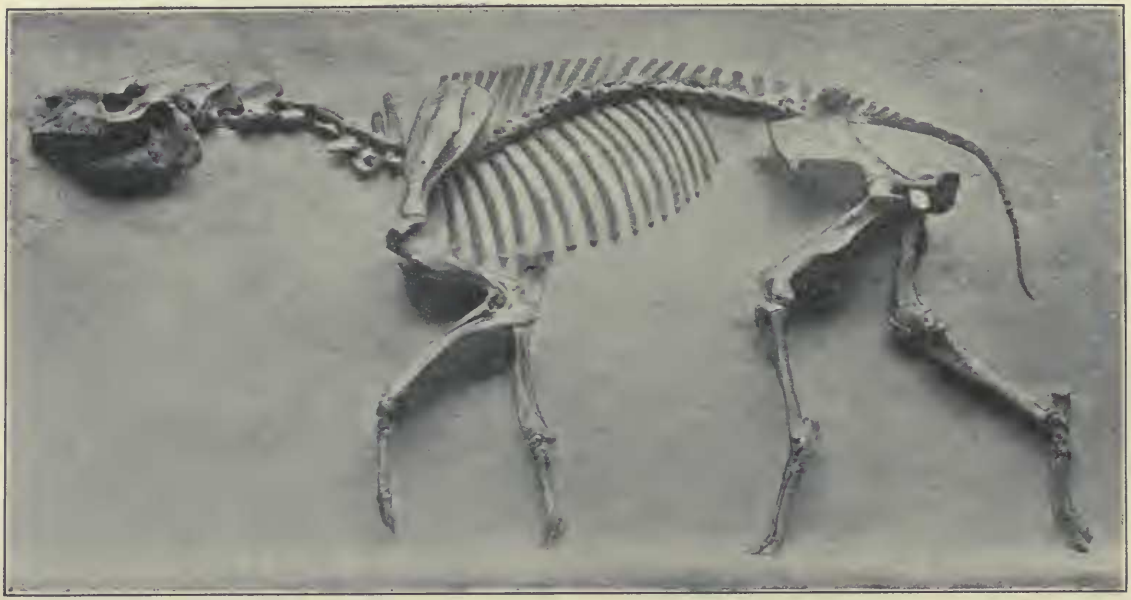

FIG. 8. The reconstructed skeleton of *Hyracodon apertus* sp. nov. Nos. 11414, 11415 Princeton University Geological Museum, standing 30¾ inches high at the shoulder and showing to advantage the cursorial adaptation of the animal.

I am unable to separate these four groups on the basis of the lower dentition. For systematic and stratigraphic purposes they may be conceived as species, although some might wish to term them subspecies. It will be noted that the distinctions between them are based primarily on structural differences in the upper posterior premolars which become increasingly molariform, the change beginning with the fourth and working forward, a situation occurring in many mammalian groups and always regarded as indicative of progressive evolution. No intermediate stages between these four types of structure in p^4 have been observed and, in the absence of blending, they are probably to be regarded as distinct species, on the basis of constant association of constant differences. Whether these slight differences in dental structure were accompanied by sexual antipathy between the various types is, of course, outside the realm both of palæontology and available data. It is possible that the four types were derived from each other in the order mentioned, ancestor and descendant continuing to exist contemporaneously for a time (see table showing vertical range). Other assumptions are equally possible.

In groups A, B and C there is a sequence of size variations, intergrading by small increments, so that size must be ruled out for purposes of specific discrimination unless we are content to change the name every few millimeters.

Nomenclature and Synonymy.

In specific nomenclature there exists some confusion which, I believe, can now be eliminated. There can be no question that the tooth structure described in A and illustrated in Fig. 1 is identical

Fig. 1. *Hyracodon arcidens,* No. 12518 Princeton University Geological Museum. Upper premolar-molar series of the left side, crown view, three fourths the natural size.

with that shown in a specimen from the Titanotherium beds at Bone Coulee, Cypress Hills, Saskatchewan, and designated by Lambe[2] *Hyracodon priscidens*. Cope's[3] brief characterization of *Hyracodon arcidens* makes it evident that he had before him a specimen showing the same features as does our No. 12518 (Fig. 1) from the zone of rusty nodules, forty feet, more or less, above the base of the Oreodon beds in Indian Creek, Pennington County, South Dakota. Similarly, Troxell's *Hyracodon arcidens mimus*[4] from the Oligocene at Deadwood, South Dakota, and his *Hyracodon selenidens*[5] from the Middle Oligocene of Colorado are size variants within the same structural range. Cope's *Hyracodon arcidens* must take priority. The holotype of this species seems to be misplaced, as the specimen so recognized by the American Museum (No. 6309, Am. Mus. Nat. Hist.) and figured as the holotype in the Cope plates[6] does not agree with Cope's description of the specimen on which his species was based. The so-called holotype, from the Cedar Creek beds (Oreodon zone) of Logan County, Colorado, is an old individual with the crown patterns of the premolars obliterated by wear and is practically indeterminate specifically. *Hyracodon priscidens* Lambe, *H. arcidens mimus* Troxell and *H. selenidens* Troxell take precedence in the order given.

The various specimens of what we may now speak of as *Hyracodon arcidens,* when arranged in order of size, are seen to intergrade by small increments as follows:

Cope's type .....premolar series, length 72 mm.[7]
Princeton Geol. Mus. No. 10816 .....premolar series, length 71.5
Princeton Geol. Mus. No. 12518 .....premolar series, length 67
H. arcidens mimus, Yale P. M. No. 11174 ....premolar series, length 67[8]
Lambe's type of *H. priscidens* .....premolar series, length 57[9]
H. selenidens, Yale P. M. No. 11173 .....premolar series, length 57[8]

[2] L. M. Lambe, *Trans. Royal Society of Canada,* second series, 1905–6, Vol. XI., Section IV., pp. 37–42, Plate I, issued August, 1905.

[3] E. D. Cope, Palæontological Bulletin No. 15, p. 2, issued August 29, 1873.

[4] E. L. Troxell, *loc. cit.,* p. 36.

[5] Ibid., p. 37.

[6] Hitherto Unpublished Plates of Tertiary Mammalia and Permian Vertebrata. U. S. G. S. and *Am. Mus. Nat. Hist.,* 1915, Plate CII. I am told that this specimen was marked as the type on Cope's label which accompanied it.

There are comparatively few specimens available of this species. Additional ones would undoubtedly afford a larger series of size variants and close some of the gaps, but even those listed above are sufficient to show intergradations by less than ten per cent. in some cases

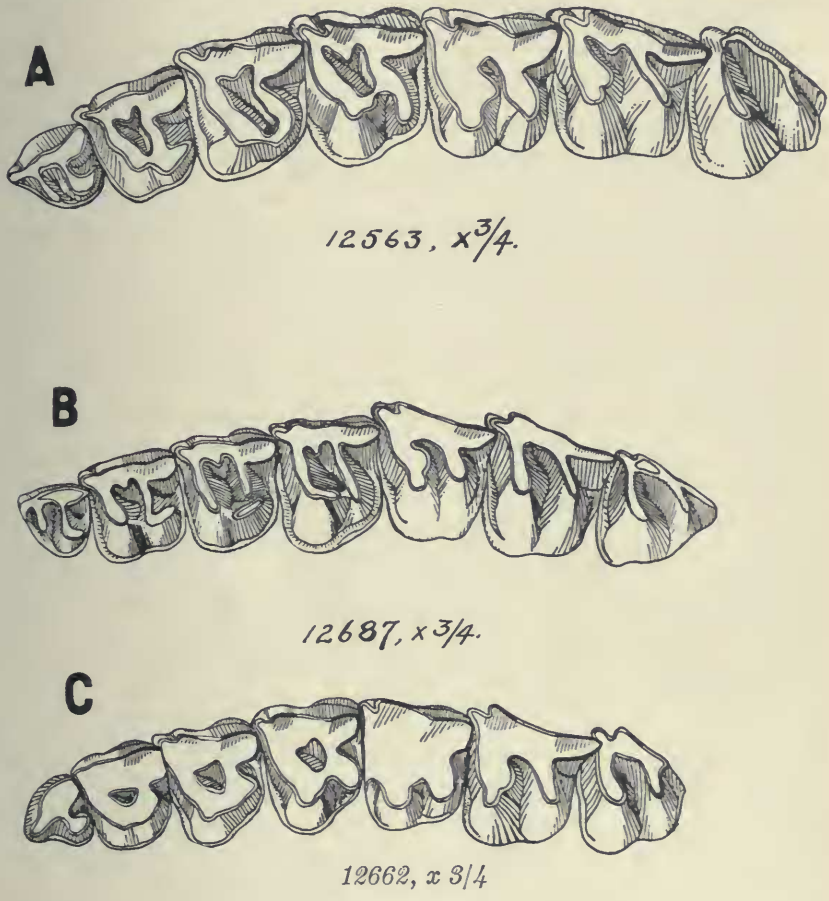

FIG. 2. *A*, maximum, *B*, intermediate and *C*, minimum size variants of *Hyracodon nebrascensis*. Upper premolar-molar series of the left side in crown view, three fourths the natural size. Specimens No. 12563, 12687, 12662 Princeton University Geological Museum.

[7] Measurements given by Cope in type description.

[8] Measurements given by Troxell, loc. cit., p. 40.

[9] Scaled from Lambe's "natural size" figure, loc. cit., Plate I. His table of measurements in the text (p. 40) gives 62 mm. for this dimension. If this is correct, there are intergradations of less than 10 per cent. throughout in the variation series listed above.

and a little under twenty per cent. in others.[9] In view of similar, but more complete, series of intermediates to be discussed in the paragraphs to follow, I feel that we are here dealing with individual variations and recognize but one species possessing the characters described under A and shown in Fig. 1, which, I suggest, we agree to call *Hyracodon arcidens* Cope.

Turning now to the tooth structure described under B and shown in Fig. 2 *A–C,* to specimens showing which I believe Leidy's name *Hyracodon nebrascensis* is applicable, it is quite true, as Mr. Troxell points out, that the original description was without figures (many of them were at that date), and that the drawings accompanying Leidy's memoir on "The Ancient Fauna of Nebraska" show, as Mr. Troxell observes, "a widely diversified group." While Dr. Leidy did not always designate his early types in subsequent publications dealing with them, he frequently figured them there carefully, and, in this particular case, his reference to the type specimen is sufficiently detailed to make its identification from the figures practically certain, as will appear from the following considerations:

Mr. J. W. Gidley has kindly placed at my disposal a so-called "type" of *Hyracodon nebrascensis* preserved in the United States National Museum (No. 138 of their vertebrate palæontological collection). This is the specimen figured on Plate XII*A,* Fig. 6, of Leidy's "Description of the Remains of Extinct Mammalia and Chelonia" from D. D. Owen's "Report of a Geological Survey of Wisconsin, Iowa and Minnesota; and Incidentally of a Portion of Nebraska Territory," Philadelphia, 1852. Comparison of the specimen with Fig. 13 of Plate XIV., "Ancient Fauna," will show that it is the same as the one there figured, for the artist has faithfully rendered certain minor breaks in the teeth which make identification unquestionable, but the drawing, as reproduced, is a little smaller than the natural size. In the first of the publications just referred to, Leidy states that "this species was first established upon the anterior portion of a skull and lower jaw, containing all the molar teeth of an old individual belonging to the collection of the Smithsonian Institution." He then goes on to mention two specimens in Dr. Owen's collections (which are again referred to in the text of the "Ancient Fauna," p. 86), "a head of the same species, of a very old

individual, with the upper part of the whole length broken away," which "contains all the molars nearly perfect," with "the crowns worn nearly to the edge of the alveoli," and "also in the same collection a face very much mutilated, except the forehead, of an individual which had just reached adult age" and which "contains all the molars nearly perfect, the last one about two thirds protruded." This second-mentioned specimen is the so-called "type," beyond the peradventure of a doubt, for it shows all the features enumerated by Leidy, and has been figured by him, as I have indicated, and as he states himself, in Fig. 13, Plate XIV., "Ancient Fauna."[10] The very old individual with the top of the head gone is, also according to Leidy's own statement, the original of Plate XV., Figs. 1 and 2, "Ancient Fauna."[11] On pages 86 and 87 of this memoir a list of all specimens of *Hyracodon* known up to the date of acceptance of the memoir (December, 1852) is given. Omitting all the references to fragments which, manifestly, have no connection with our endeavor to identify the type, and passing over the descriptions of the two Owen specimens, which appears in substantially the same words as have been quoted above, we find at the head of the list mention made of "the anterior portion of a skull, accompanied by the lower jaw, of an adult individual. The former has the forehead, orbital entrance, and molar teeth well preserved, but the face is very much broken and its nasal part is displaced. The lower jaw contains all the molars in perfect condition, but it has lost its rami and the symphysis." These parts are figured on Plate XIV., Figs. 1–3, and on Plate XV., Fig. 3, of the "Ancient Fauna" and are said to be from Captain Stewart Van Vliet's collection. Nothing is said about the type in the Smithsonian Institution which he had previously described in similar phrase, speaking of it as an old individual, which a glance at the plates will show the Van Vliet specimen to be. I do not regard this as an oversight, but believe that Leidy had in mind one and the same specimen, which might very well have come from Captain Van Vliet's collection and yet belong to the Smithsonian Institution.[12] Leidy's figure shows

[10] See "Ancient Fauna," page 86, third line from foot of page.

[11] See page 87, second line.

[12] Mr. Gidley is unable to supply any information regarding the present location of this specimen. No. 138 of the National Museum collection, according to Mr. Gidley, is recorded in the old catalogue as having been collected by Dr. John Evans.

an individual with well-worn teeth, but with a posterior premolar of the blocked-valley type, with deeply grooved inner tooth wall as defined under B, and of a size practically identical with No. 12687 (Fig. 2 *B*) of the Princeton collection. I, therefore, submit that Leidy's *Hyracodon nebrascensis,* in this limited sense, is entirely applicable to that sequence of individuals within the genus which has the transverse valley of p^4 blocked in the manner indicated, and that no adequate grounds exist, or have existed, for discarding the name. Figures 4–8, Plate XIV., of the "Ancient Fauna" seem to represent unworn examples of the same type.

As in the preceding species, a series of individual variants can be made out, intergrading by increments of not more than four millimeters between extremes in the length of the molar series, here taken as the basis for comparison, because present completely in all the specimens studied for dimensions. Material from the Princeton collection only is used as follows:

No. 12662, molar series,	length 57
No. 12687, molar series,	length 61
No. 12688, molar series,	length 61
No. 12666, molar series,	length 65
No. 12680, molar series,	length 67.5
No. 12563, molar series,	length 71
No. 10723, molar series,	length 72

Of these, the first five are contemporary and from a six-inch zone of rusty nodules about sixty feet (sometimes less) above the top of a similar zone affording No. 12563, which, in turn, lies some forty feet, more or less, above the base of the Oreodon beds and constitutes the lower zone of rusty nodules of our Princeton field nomenclature, while the other may be designated as the upper rusty nodular zone of the Lower Oreodon beds. No. 10723, on the other hand, is from well up in the Protoceras-Leptauchenia beds of the Upper Oligocene and is but a trifle larger than its Lower Oreodon beds predecessor. The specimen numbered 12662 (Fig. 2, *C*) is as small as Mr. Troxell's *H. selenidens,* which I regard as an individual variant of *H. arcidens,* as already indicated, for exactly the same reasons which induce me to place this small specimen of *H. nebrascensis* as a terminal size variant in the *nebrascensis* series. Each conforms to its own structural type, but intergrades by small-size increments with the largest specimens referable thereto.

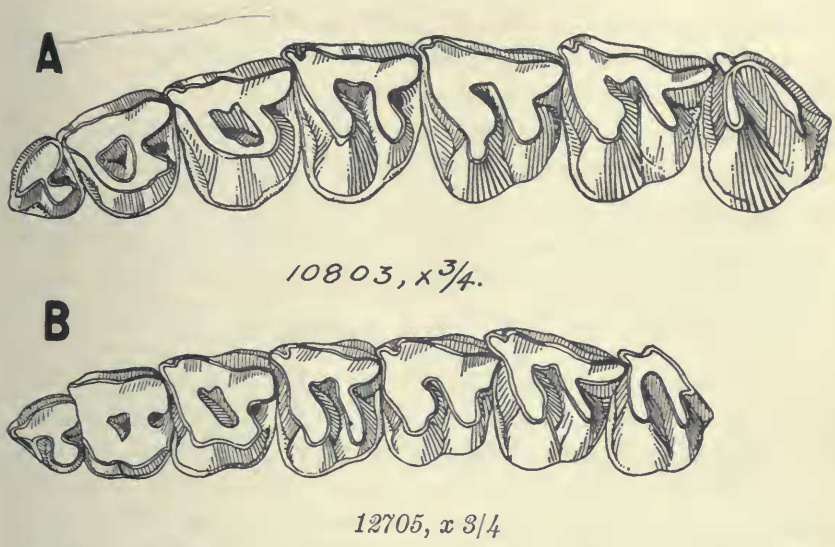

FIG. 3. *A*, maximum and *B*, minimum size variants of *Hyracodon apertus* sp. nov., of which No. 10803 is the type. Upper premolar-molar series of the left side in crown view, three fourths the natural size. No. 10803, 12705 Princeton University Geological Museum.

For the species described as C we are without a name and I propose that it be known as *Hyracodon apertus* sp. nov., with reference to the wide-open valley of p^4 as described under C above, designating as type a skull with right ramus of the lower jaw, No. 10803, Princeton University Geological Museum, collected by Mr. J. B. Hatcher in 1893 from a zone of brown nodules above the Protoceras sandstones in Corral Draw, South Dakota. A crown view of the premolar-molar series is given in Fig. 3 *A*. Regrettable as the proposing of additional specific names may be, it is unavoidable in this instance in order to designate a form already adequately figured by Leidy in Fig. 13 on Plate XIV., "Ancient Fauna," but grouped by him with *nebrascensis*, from which, however, the absence of blocking in the valley of p^4 easily separates it.[13] To this species belongs the mounted

[13] Long-continued wear would, undoubtedly, isolate a central depression as shown in Leidy's figure of *nebrascensis* ("Ancient Fauna," Pl. XV., Fig. 3) or in Fig. 2 *C*. At corresponding stages of wear, however, p^4 is unblocked in *apertus* and completely blocked in *nebrascensis* (compare Figs. 2*A* and 3*A*). The development of a transverse spur from the protoloph would convert p^4 of *apertus* into a tooth of the *nebrascensis* type; its loss in *nebrascensis* would result in the structure found in *apertus*.

skeleton in the Princeton University Geological Museum (Nos. 11414, 11415, Fig. 8) monographed some years ago by Professor Scott[14] as *Hyracodon nebrascensis.*

Here also a series of individual variants may be arranged, using the length of the molar series as our basis for comparison:

Princeton Geol. Mus. No. 12705 .....molar series, length 59
Princeon Geol. Mus. No. 12702 .....molar series, length 64
Princeton Geol. Mus. No. 11414 .....molar series, length 64
U. S. National Mus. No. 138 .....molar series, length 65[15]
Princeton Geol. Mus. No. 10803 .....molar series, length 72.5

The horizon of Leidy's specimen is unknown. Of the others, No. 12705 is from the lower zone of rusty nodules of the Oreodon beds, No. 12702 from the upper nodular zone of the same, No. 11414 from the Upper Oreodon beds, and No. 10803, the type from the Protoceras-Leptauchenia beds of the Upper Oligocene. Once more I am convinced that these are only individual variations, and that, while there is a gap of a little over ten per cent. between the last two members of the series, additional specimens, when available, will close it.

FIG. 4. *Hyracodon leidyanus,* No. 10802 Princeton University Geological Museum. Upper premolar-molar series of the left side, crown view, three fourths the natural size. The tip of m^3 appears just above the gum and is not shown in the drawing.

To the fourth species, described under D, Mr. Troxell's name, *Hyracodon leidyanus,* seems entirely applicable. In Fig. 4 is shown the upper premolar-molar series of an incomplete skull and lower jaws, No. 10802 of the Princeton collection, from the rusty nodular layer above the Protoceras sandstones in Corral Draw, in which the

[14] W. B. Scott, "Die Osteologie von Hyracodon Leidy," *Festschrift für Carl Gegenbaur,* Leipzig, 1896. Pp. 353–384. Three plates.

[15] In Fig. 13, Pl. XIV., "Ancient Fauna," this dimension is 62 mm., showing that the figure is not quite natural size.

third molar is just appearing above the gum. In Fig. 5 a very much older individual (No. 10144, Princeton University Geological Museum) is seen, in which the open valley is retained in both the third and fourth premolars, both of which are well worn, as are also the anterior molars. The third molar is fully erupted and partly worn. Both these specimens are fractured in such a way as to show the absence of germs of replacement teeth above the posterior premolars and I can not escape the conclusion that we are here dealing with per-

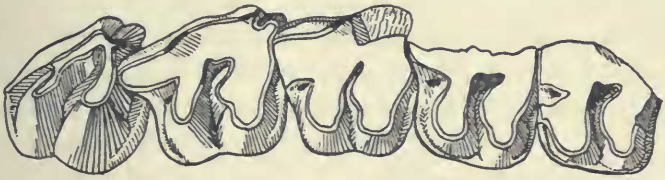

FIG. 5. *Hyracodon leidyanus*, No. 10144 Princeton University Geological Museum. Upper premolar-molar series from p^3–m^3 of the right side, crown view, three fourths the natural size.

manent teeth. In *Hyracodon* the milk dentition is more advanced in crown-pattern development than are the permanent premolars, even milk p^2 having an unblocked transverse valley (Figs. 6, 7). These molariform milk teeth have lower crowns and thinner enamel than their successors, and in p^2 there is a prominent style from the cingulum at the entrance of the transverse valley. Mr. Gidley has called my attention to certain specimens in his charge in which no germ teeth of the replacement series appear beneath the milk premolars and suggests that they "were very late in forming, but when started grew very rapidly to replace the milk dentition which seems sometimes to have persisted until all the true molars have come into use."[16]

FIG. 6. *Hyracodon* sp., No. 12679 Princeton University Geological Museum. Milk dentition and m^1 and ^{2} of the left side, crown view, three fourths the natural size. M^3 had germinated but is not preserved with the other teeth. Germs of the replacement series appear in the maxillary above the first and third milk premolars.

[16] Personal letter.

This is probable, as shown by our No. 12679, but I do not feel justified in regarding the well-worn premolars of our No. 10144 as persistent milk teeth and so have accepted without question Mr. Troxell's species.[17] Some doubt seems to exist about the stratigraphic position of his type specimen which is stated to be from the Middle or Lower Oligocene, Crow Buttes, South Dakota. The first-mentioned Princeton specimen occupies the stratigraphic position which might be expected for such an advanced form, which, so far as anyone can say at present, may range into lower beds and even occur in the Lower Oligocene, a question which can be settled only by further collecting. The second Princeton specimen was obtained by the Expedition of 1882 and is from the White River Oligocene of South Dakota, occurring in a matrix resembling that of the Leptauchenia beds, but no further information is available regarding its stratigraphic position. As there are but three specimens of *Hyracodon leidyanus* so far available, which agree closely in dimensions, no series of size variants can be recognized.

FIG. 7. *Hyracodon* sp. No. 3758 United States National Museum. First to third milk premolars of the right side, crown view, three fourths the natural size. No germs of the replacement series have formed above these teeth

Of the other species discussed by Mr. Troxell, *"Hyracodon" planiceps*[18] appears among the rhinocerotidæ in Dr. Matthew's faunal

[17] The milk dentition shown in Fig. 6 has the crown-patterns of the premolars more obliterated by wear than in m^1 and the necks of these teeth are farther below (*i.e.*, ventral to) the alveolar border than is true of the first molar, showing that they were erupted and in use before the appearance of that tooth. In Nos. 10802 and 10144 (Figs. 4 and 5), the first molar is abraded to a greater degree than the two preceding premolars and the necks of the tooth crowns are approximately on the same level, demonstrating that the premolars appeared after the eruption of m^1 and are of the replacement series. Mr. Troxell's drawing of *H. leidyanus* shows m^1 more extensively abraded than the premolars, so that their character as permanent teeth is fully established. Dr. Matthew has kindly called my attention to these criteria.

[18] W. D. Matthew, "Cenozoic Mammal Horizons of Western North America," Bulletin 361, U. S. G. S., in collaboration with Professor Osborn, p. 105, 1909.

lists published as far back as 1909. *Hyracodon major,* if properly referable to the genus, is specifically indeterminate and should be abandoned. The type consists of some skeletal elements in the Princeton collection, No. 10001, of unknown stratigraphic position other than that they are from the White River Oligocene of Dakota, and may be a little larger than the corresponding skeletal parts of the largest individuals of certain of the species here recognized. It is possible that still larger individuals of these existed than have so far appeared in the collections, but the diagnostic characters for their specific determination must depend, in any event, on the upper premolars and not on the skeleton.

This completes a survey of the nomenclature and synonymy of the genus to date.

Range in Time.

The following table shows the range of species in time and includes several specimens from the American Museum collection, not referred to in the text, kindly placed at my disposal by Professor Osborn and Dr. Matthew. It will be seen at once that each one of the four species recognized is not confined to a definite zone, but overlaps widely, in turn, on the time limits of the next and more advanced type. If Mr. Troxell is correct in placing *H. leidyanus* as low as the Titanotherium beds, it may well be that the divergence of all four species took place there, or even earlier, before the appearance of *Hyracodon* in the North American non-marine Oligocene of the plains region, to which it is, so far, narrowly confined and of which it is an excellent index fossil. For zonal purposes the species are of little value, as they range through a considerable thickness of beds, and the same is also true of the size variants.

In this table the heavy black lines show the position of the lower and upper zones of rusty nodules in the Lower Oreodon beds, both of which are properly included in the *Mesohippus bairdii-Oreodon culbertsoni* zone, the upper and lower limits of which have not yet been established. The specimens discussed in the table are from the following localities:

Hyracodon arcidens Cope.

8807 Am. Mus. Nat. Hist. Oreodon beds, probably upper according to Dr. Matthew, Logan Co., Colorado.

Species.			A. *H. arcidens* Cope.	B. *H. nebrascensis* Leidy.	C. *H. apertus* sp. nov.	D. *H. leidyanus* Troxell.
Protoceras-Leptauchenia Beds				P. 10723	P. 10803 8811 Am. Mus. Nat. Hist. (almost identical in size with P. 12705)	P. 10802
Upper Oreodon Beds			8807 Am. Mus. Nat. Hist. (exact size of P. 12518)		P. 10978 P. 11414	
		?				
Lower Oreodon Beds	*Mesohippus bairdii–Oreodon culbertsoni* zone, limits not yet established	60′ or less		P. 12666, 12680, 12687, 12688 P. 12662	P. 12702	
			P. 12518	P. 12563	P. 12705	
		40′ ±				
		?				
Titanotherium Beds			Lambe's Type of *H. priscidens* = *H. arcidens* Cope			

12518 Princeton. Lower zone of rusty nodules, Lower Oreodon beds, Indian Creek, Pennington Co., South Dakota.

Lambe's type of *H. priscidens*. Titanotherium beds, Bone Coulee, Cypress Hills, Assiniboia.

Hyracodon nebrascensis Leidy.

10723 Princeton. Brown nodular layer above upper sandstones of Protoceras beds, Corral Draw, South Dakota.

12662 Princeton. Fifteen feet below upper zone of rusty nodules, Lower Oreodon beds, Corral Draw, South Dakota.

12666, 12687, 12688, 12680 Princeton. Upper zone of rusty nodules, Lower Oreodon beds, Quinn Draw, South Dakota.

12563 Princeton. Lower zone of rusty nodules, east part of Indian Creek basin, Pennington Co., South Dakota.

Hyracodon apertus sp. nov.

10803 Princeton. Brown nodules above the Protoceras sandstone, Corral Draw, South Dakota.

10978 Princeton. Upper Oreodon beds, Quinn Draw, South Dakota.

11414 Princeton. Upper Oreodon beds, South Dakota.

12702 Princeton. Upper zone of rusty nodules, Lower Oreodon beds, Quinn Draw, South Dakota.

12705 Princeton. Lower zone of rusty nodules, Lower Oreodon beds, Corral Draw, South Dakota.

Hyracodon leidyanus Troxell.

10802 Princeton. Brown nodule layer above Protoceras sandstones, Corral Draw, South Dakota.

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